# ON COUPLING OF CERTAIN SEX–LINKED CHARACTERS IN DROSOPHILA.

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In the course of his experiments on the modes of inheritance in *Drosophila*, Morgan has called attention[1] to the fact that when flies bearing two or more pairs of characters of certain sorts are crossed, these characters appear in the $F_2$ generation coupled as in the original combination (*i. e.*, in the grandparents). This coupling is not complete, but is much larger than is to be expected if the different pairs of characters were independently mendelizing. In a letter to me last autumn he suggested that " in order to find out if there is here some deep-lying principle or only some irregularity, it will be necessary to obtain very large numbers of the $F_2$'s; let us say ten or twenty thousand."

Morgan has offered an explanation·of this coupling[2] on the supposition that the factors concerned in the production of the characters lie near together in the chromosomes, and that the twisting of homologous chromosomes about each other in the strepsinema stage of gametogenesis which causes both maternal and paternal characters to lie on each side of the double chromosome, does not separate certain factors that lie very close together, so that when the chromosomes split, these factors will both occupy the same gamete.

It was in order to test these theories that I undertook, at Dr. Morgan's suggestion, to raise " large numbers of the $F_2$'s."

Dr. Morgan's kindly advice and aid have helped me a great deal in this work. I wish also to record here and express my appreciation of the enthusiastic assistance of Miss Margueritte Harmon and Mr. Felix Gustafson, without whose aid the work could not have been done at this time.

I began with pure stock of *Drosophila* of two kinds: Flies with normal body color and red eyes (this is the normal wild fly),

and flies with a yellow body and white eyes; both stocks were sent to me by Morgan. The origin of these mutations, and the facts of their individual inheritance, have been described by Morgan[1] in earlier papers.

In speaking of the flies from this time on, I shall use the letter $N$ to signify the presence of the factor for normal body color, $Y$ for yellow body color, $R$ for red eye, and $W$ for white eye. Of these factors, $N$ is dominant over $Y$, and $R$ over $W$. The factors $N$ and $R$ are only found in association with the $X$-chromosomes, which is duplex in the female but simplex in the male. This means, of course, that $N$ and $R$, as used here, are sex-linked characters. It is not necessary to assume that any of these factors are units but that they act as units in the following experiments.

According to the theory to be tested we have the following data as to the gametic constitution of the flies. A pure $NR$ female has the constitution $NRX—NRX$, and all her gametes bear the factors, $NRX$. A pure $NR$ male has the constitution $NRX—YW$, and the sperms bear either of two combinations of factors, $NRX$ or $YW$. A pure $YW$ female has the constitution $YWX—YWX$; the gametes all bear $YWX$. The pure $YW$ male has the constitution $YWX—YW$, and his gametes bear either $YWX$ or $YW$.

## EXPERIMENT I.

In experiment I, a pure $NR$ female was crossed to a pure $YW$ male. The results to be expected in the $F_1$ and $F_2$ generations if eye color and body color are independently mendelizing, are shown in Table I.

## TABLE I.

| | | |
|---|---|---|
| $P_1$. | $NRX—NRX = NR♀$ | $YWX—YW = YW♂$ |
| | Gametes   $NRX$ | $YWX$,  $YW$ |
| $F_1$. | $NRX—YWX = NR♀$ | $NRX—YW = NR♂$ |
| | Gametes (1) $NRX$, (2) $YWX$, | $NRX$,  $YW$ |
| | (3) $YRX$, (4) $NWX$ | |
| $F_2$. | $NRX—NRX = NR♀$ | $NRX—YW = NR♂$ |
| | $YWX—NRX = NR♀$ | $YWX—YW = YW♂$ |
| | $YRX—NRX = NR♀$ | $YRX—YW = YR♂$ |
| | $NWX—NRX = NR♀$ | $NWX—YW = NW♂$ |

[1] *Science*, July 22, 1910. p. 120; *Science*, March 31, 1911, p. 496; *Jour. Exper.* *Zoöl.*, November, 1911, p. 365.

This table shows that all members of the $F_1$ generation should have the appearance of normal $NR$'s.   In my experiments, this was true without exception.

The females of the $F_1$ generation should produce four classes of eggs, representing all combinations of $N$, $R$, $Y$ and $W$.   The males should produce sperms of two classes.   The combination of these gametes should produce in the $F_2$ generation equal numbers of males and females, but all of the females should be $NR$, while one fourth of the males should belong to each of the following classes: $NR$, $YW$, $YR$, $NW$.

If, on the contrary, the $N$ and $R$ are completely coupled we have the same result in the $F_1$ generation, but the gametes of the $F_1$ females would be of two classes only, viz., $NRX$ and $YWX$, while those represented in the table by (3) and (4) would be absent.   Therefore there would occur in the $F_2$ generation $NR$ females as before, and only two kinds of males, one half being $NR$ and the other half $YW$.

Table II. shows the actual results of this experiment.   From 24 bottles I raised 11,394 flies.   Of these 6,081 were females. All but one of these females were $NR$.   The other was $NR$ on the left side and $YW$ on the right, and may be for present purposes ignored[1] as an anomaly.   Of the males there were of class $NR$, 2,870; class $YR$, 34; class $NW$, 36; class $YW$, 2,373. Whatever the explanation may be, it is obvious that coupling has occurred.   It is equally obvious that the coupling is not complete.

The result for the individual bottles accorded with that of the total.   There is in every bottle except number 6, a larger number of $NR$ males than of $YW$ males.   This is without doubt due to a greater vitality in the normal flies than in the mutants, for also in the pure cultures the normal flies are much more fertile than the others.   This matter is discussed by Morgan in one of the papers mentioned[2] above, under the heading, "The Fertility of Deficient Mutations."   I have no reason to dissent from the statements made there.   The reasons for this infer-

[1] This fly was active and except for color appeared to be normal.   I attempted to mate her to $YW$ males, but she appeared to be sterile, and after two weeks she was preserved for histological study.

[2] *Jour. Exper. Zoöl.*, Nov., 1911.

tility are now being investigated. At present, at least, the fact is very apparent, not only in my own results, but also in those published by Morgan.

## TABLE II.

### TABLE SHOWING RESULTS OF EXPERIMENT I.

| Bottle No. | $NR\,♀$. | $NR\,♂$. | $YR\,♂$. | $NW\,♂$. | $YW\,♂$. | Total. | |
|---|---|---|---|---|---|---|---|
| 1 | 201 | 92 | 4 | 3 | 81 | 381 | |
| 2 | 161 | 89 | 1 | 1 | 77 | 329 | |
| 3 | 282 | 123 | 1 | 1 | 90 | 497 | |
| 4 | 351 | 155 | 0 | 3 | 127 | 636 | |
| 5 | 46 | 28 | 1 | 1 | 18 | 94 | |
| 6 | 96 | 37 | 0 | 0 | 40 | 173 | |
| 9 | 108 | 46 | 1 | 0 | 33 | 188 | |
| 10 | 267 | 147 | 5 | 0 | 126 | 545 | |
| 13 | 253 | 144 | 0 | 1 | 84 | 482 | |
| 14 | 183 | 104 | 1 | 1 | 72 | 361 | |
| 15 | 253 | 144 | 1 | 1 | 135 | 534 | |
| 17 | 317 | 143 | 1 | 2 | 123 | 586 | |
| 19 | 352 | 165 | 1 | 2 | 132 | 652 | |
| 20 | 292 | 121 | 3 | 3 | 104 | 523 | |
| 21 | 277 | 146 | 2 | 1 | 102 | 528 | |
| 22 | 280 | 114 | 0 | 0 | 99 | 493 | |
| 23 | 136 | 63 | 0 | 0 | 72 | 271 | |
| 24 | 160 | 80 | 0 | 1 | 59 | 300 | |
| 25 | 127 | 73 | 2 | 0 | 55 | 257 | |
| 26 | 242 | 118 | 0 | 0 | 64 | 424 | |
| 27 | 544 | 234 | 3 | 2 | 233 | 1,016 | 1 abnormal ♀ |
| 50 | 503 | 203 | 5 | 8 | 153 | 872 | $\frac{1}{2}NR, \frac{1}{2}YW$ |
| 51 | 325 | 154 | 0 | 3 | 148 | 630 | |
| 52 | 324 | 147 | 2 | 2 | 146 | 621 | |
| Totals | 6,080 | 2,870 | 34 | 36 | 2,373 | 11,393 | 11,394 |

## EXPERIMENT II.

In this experiment, the reverse cross was made, viz., pure $YW$ females by pure $NR$ males. According to the theory if no coupling occurred, the $F_1$ and $F_2$ generations should give the results shown by Table III.

## TABLE III.

$P_1$.    $YWX—YWX = YW\,♀$          $NRX—YW = NR\,♂$
  Gametes $YWX$                    $NRX, YW$

$F_1$.    $NRX—YWX = NR\,♀$          $YWX—YW = YW\,♂$
  Gametes (1) $NRX$, (2) $YWX$,      $YWX, YW$
    (3) $YRX$, (4) $NWX$

$F_2$.    $NRX—YWX = NR\,♀$          $NRX—YW = NR\,♂$
  $YWX—YWX = YW\,♀$          $YWX—YW = YW\,♂$
  $YRX—YWX = YR\,♀$          $YRX—YW = YR\,♂$
  $NWX—YWX = NW\,♀$          $NWX—YW = NW\,♂$

The table shows that in the $F_1$ generation there should be only *NR* females and *YW* males. My studies completely bore out this conclusion.

As in the previous experiment, the females of the $F_1$ generation should produce four classes of eggs, representing the various combinations of the factors concerned. The males should produce two classes of sperms. The union of these gametes should produce in the $F_2$ generation equal numbers of males and females of the four classes, *NR*, *YW*, *YR*, *NW*.

Complete coupling would give only two classes of eggs and hence only two classes of males and females, viz., *NR* and *YW*. Table IV. shows the results actually obtained. From 24 bottles there hatched 9,626 flies, distributed as follows: *NR* females, 2,761; *NR* males, 2,462; *YR* females, 30; *YR* males, 29; *NW* females, 21; *NW* males, 24; *YW* females, 2,204; *YW* males, 2,095.

Here again the coupling occurs, and again the coupling is not complete. We find also the deficiency of males and of mutants

TABLE IV.

GIVING RESULTS OF EXPERIMENT II.

| Bottle No. | *NR* ♀. | *NR* ♂. | *YR* ♀. | *YR* ♂. | *NW* ♀. | *NW* ♂. | *YW* ♀. | *YW* ♂. | Total. |
|---|---|---|---|---|---|---|---|---|---|
| 7 | 101 | 74 | 0 | 0 | 0 | 4 | 102 | 76 | 357 |
| 8 | 46 | 48 | 2 | 0 | 0 | 0 | 40 | 36 | 172 |
| 11 | 63 | 63 | 0 | 0 | 3 | 0 | 64 | 68 | 261 |
| 12 | 87 | 80 | 1 | 2 | 1 | 0 | 67 | 75 | 313 |
| 16 | 74 | 88 | 1 | 0 | 0 | 3 | 79 | 80 | 325 |
| 29 | 82 | 81 | 0 | 1 | 1 | 1 | 86 | 77 | 329 |
| 31 | 206 | 168 | 1 | 5 | 0 | 1 | 176 | 161 | 718 |
| 32 | 126 | 111 | 0 | 2 | 1 | 3 | 122 | 120 | 485 |
| 33 | 139 | 130 | 5 | 1 | 0 | 2 | 112 | 137 | 526 |
| 34 | 153 | 152 | 1 | 1 | 2 | 1 | 116 | 101 | 537 |
| 35 | 76 | 42 | 0 | 0 | 0 | 3 | 19 | 31 | 171 |
| 36 | 78 | 55 | 0 | 1 | 0 | 1 | 56 | 51 | 242 |
| 37 | 75 | 74 | 1 | 0 | 0 | 0 | 56 | 64 | 270 |
| 39 | 48 | 39 | 0 | 2 | 0 | 0 | 30 | 24 | 143 |
| 40 | 46 | 45 | 0 | 0 | 0 | 0 | 41 | 43 | 175 |
| 54 | 114 | 103 | 4 | 4 | 2 | 0 | 96 | 81 | 404 |
| 55 | 119 | 100 | 1 | 1 | 1 | 1 | 78 | 74 | 375 |
| 56 | 178 | 156 | 2 | 1 | 3 | 1 | 138 | 153 | 632 |
| 57 | 137 | 118 | 1 | 2 | 2 | 0 | 118 | 104 | 482 |
| 58 | 183 | 181 | 3 | 3 | 1 | 0 | 152 | 130 | 653 |
| 59 | 184 | 143 | 0 | 0 | 1 | 0 | 139 | 100 | 567 |
| 60 | 202 | 190 | 5 | 2 | 1 | 0 | 160 | 156 | 716 |
| 61 | 195 | 153 | 1 | 1 | 1 | 3 | 121 | 124 | 599 |
| 62 | 49 | 58 | 1 | 0 | 1 | 0 | 36 | 29 | 174 |
| Total | 2,761 | 2,462 | 30 | 29 | 21 | 24 | 2,204 | 2,095 | 9,626 |

when compared with the normal females. The figures in either
of these experiments show an average of about eighty-five indi-
viduals in which the coupling persists to one in which the factors
are interchanged.

## EXPERIMENT III.

After carrying the above experiments to near their conclusion
I suspected that perhaps there was some reason unknown to me
which made $N$ naturally couple with $R$, no matter what the
original combination might have been. That my suspicions
were ill-founded was demonstrated by the following experiments.

In the first of these, I selected from the classes of $NW$ females
and $YR$ males of the $F_2$ generation (Table III.) obtained in
Experiment II., virgin individuals and mated them. The
gametic constitution of these and the nature of their offspring
according to the theory are shown in Table V.

### TABLE V.

THE $P_1$ GENERATION OF THIS TABLE CONSISTS OF MEMBERS OF THE $F_2$ GENERATION
OF EXPERIMENT II.

$P_1$.  $NWX—YWX = NW♀$          $YRX—YW = YR♂$

Gametes $NWX, YWX$               $YRX,  YW$

$F_1$  (1) $NWX—YRX = NR♀$       (3) $NWX—YW = NW♂$

    (2) $YWX—YRX = YR♀$       (4) $YWX—YW = YW♂$

This table shows that equal numbers of $NR$ females, $YR$ fe-
males, $NW$ males, and $YW$ males should be produced. I ob-
tained:

        $NR$ females, 45                $NW$ males, 52

        $YR$ females, 50                $YW$ males, 47

I now took some of the virgin females from the $NR$ group and
inbred them to the $YW$ males. It should be recalled that the
parents of the $F_2$ generation in Experiment II. were also of these
classes, and therefore, as shown by Table VI., if body color and
eye color were not to couple, we should expect the same classes
of individuals in the $F_2$ generation in each case. If coupling
occurred here (i. e., if having " broken " once, should not give
any tendency to do so again), we should expect here, not the
same results as those obtained in the previous experiment, but
rather that the classes that were then small should now be the
large classes, while the large ones should be now small.

I started six bottles of this cross, and in every case the classes $YR$ and $NW$ were in the majority. But in five of the bottles the food was very wet and the hatch poor. None of them gave any $YW$'s at all. Also, in every case the class $NW$ far outnumbered the class $YR$. In the sixth bottle (see Table VII., Bottle No. 44) the food was in better condition (*i. e.*, was drier), the hatch larger, the ratios nearer the expected, and class $YW$ represented. This would seem to indicate some relation between the dark body color and the relative dampness of the food, though I realize that this suggestion requires further investigation.

### TABLE VI.

The members of $F_1$ are taken from classes (1) and (4) of Table V.

$F_1$.     $NWX—YRX = NR ♀$                  $YWX—YW = YW ♂$
Gametes (1) $NRX$,   (2) $YWX$,              $YWX$,  $YW$
           (3) $YRX$,   (4) $NWX$

$F_2$.   $NRX—YWX = NR ♀$                   $NRX—YW = NR ♂$
       $YWX—YWX = YW ♀$                   $YWX—YW = YW ♂$
       $YRX—YWX = YR ♀$                   $YRX—YW = YR ♂$
       $NWX—YWX = NW ♀$                   $NWX—YW = NW ♂$

### TABLE VII.

#### GIVING RESULTS OF EXPERIMENT III.

| Bottle No. | $NR ♀$. | $NR ♂$. | $YR ♀$. | $YR ♂$. | $NW ♀$. | $NW ♂$. | $YW ♀$. | $YW ♂$. | Total. |
|---|---|---|---|---|---|---|---|---|---|
| 41 | 1 | 1 | 17 | 19 | 63 | 37 | 0 | 0 | 138 |
| 42 | 2 | 1 | 10 | 6 | 66 | 55 | 0 | 0 | 140 |
| 43 | 1 | 0 | 3 | 1 | 44 | 47 | 0 | 0 | 96 |
| 44 | 0 | 2 | 91 | 90 | 103 | 115 | 2 | 0 | 403 |
| 45 | 1 | 1 | 9 | 13 | 41 | 25 | 0 | 0 | 90 |
| 46 | 0 | 3 | 11 | 7 | 74 | 40 | 0 | 0 | 135 |
| Total | 5 | 8 | 141 | 136 | 391 | 319 | 2 | 0 | 1,002 |

That the coupling here is in accord with that of the previous experiments is clear. A study of bottle number 44 in which the food was not wet and sticky will present an even fairer view of the case, as well as one in which the results are nearer those expected.

### EXPERIMENT IV.

Here again I selected from virgin members of the $F_2$ generation of Experiment II., this time crossing $YR$ females and $NW$ males.

Their supposed gametic constitution and the results to be expected in the $F_1$ generation are shown in Table VIII.

## TABLE VIII.

The $P_1$ generation consists of members of the $F_2$ generation of Experiment II. (see Table III.).

$P_1$.    $YRX$—$YWX = YR \female$              $NWX$—$YW = NW \male$
Gametes  $YRX, YWX$                            $NWX, YW$

$F_1$.  (1) $YRX$—$NWX = NR \female$        (3) $YRX$—$YW = YR \male$
    (2) $YWX$—$NWX = NW \female$        (4) $YWX$—$YW = YW \male$

The table shows that there should be produced in equal numbers $NR$ females, $NW$ females, $YR$ males, and $YW$ males. The actual hatch consisted of

$NR$ females, 116              $YR$ males,   82
$NW$ females, 116              $YW$ males, 100
                               $NW$ males,    2

I am quite unable to account for the occurrence of the two $NW$ males, except through mutation. Rather than offer this rather wild guess, I shall not attempt to explain it at all. It will be observed, however, that it could not possibly have been that the $YR$ females were not virgin when the experiment was begun, for no known mating will produce an $NW$ male from such a female. Also, it would be an unbelievable coincidence that should produce on the same day—the fifth after the beginning of the hatch—two such males on account of contamination of the food.

As in experiment III., I mated the virgin $NR$ females to the $YW$ males, so that Table VI. accounts for the results in the $F_2$ generation in the same way that it did for experiment III. The discussion, also, of the probabilities for the $F_2$ generation in that experiment applies equally well to this experiment.

I started only one bottle of this kind (No. 47). From it were produced:

$NR$ females, 2;   $YR$ females, 81;   $NW$ females, 89;   $YW$ females, 1;
$NR$ males,   1;   $YR$ males,   82;   $NW$ males,   90;   $YW$ males,   0.

A comparison of these figures with those of bottle No. 44 of experiment III. will show a very close agreement of the one to the other.

## DISCUSSION OF THE PROBLEM IN THE LIGHT OF THE EXPERIMENTS.

In the above experiments we find Morgan's observations verified.

1. A coupling occurs in the $F_2$ generation in which the coupled factors are those that were associated in the grandparents.

2. This coupling is by no means complete.

3. The females of any class as a rule outnumber the males.

4. The classes which lack the factor for red eye or normal body color contain a smaller number of individuals than those which possess this factor, and the class lacking both of them is the smallest of all.

Perhaps the last two conclusions may be stated: The vitality of any class of individuals is increased according to the number they possess of factors found in the normal ($NR$) female. On this assumption, the reason why the $NR$ males are less numerous than the $NR$ females would be accounted for by their having the simplex rather than the duplex gametic constitution. Perhaps an individual has an added vitality even through the possession of two rather than one of the factors for sex, as in the case of the $YW$ females as opposed to the $YW$ males. I do not desire to urge the case, particularly since I understand Morgan is conducting investigations that will throw more light on the subject.

The particular problem presented by these experiments is to explain why the coupling occurs but is not complete. This problem perhaps can be finally settled only by the cytologist.

Morgan's suggestion, based on the observations of Jannsens, on the twisting of the chromosomes, I understand as follows. The factors through the influence of which any particular character appears in an individual, are represented in the chromosomes by material particles which have always the same relative linear position. " When the parental pairs (in the heterozygote) conjugate, like regions will stand opposed. There is good evidence to support the view that during the strepsinema stage, homologous chromosomes twist around each other, but when the chromosomes separate (split), the split is in a single plane."[1]

[1] Morgan, in *Science*, Sept. 22, 1911, p. 384.

Now the supposition is that if two of the factors lie close together on the same side of the double chromosome, they may escape separation by the splitting. This means that the factors must be closer together than half the distance around one complete turn of the spirally twisted chromosomes. This length is the maximum possible in order to allow two factors to be coupled on account of proximity. This length might be indefinitely diminished so that many factors of one of the parental chromosomes might lie closely approximated on the same side of the split, and therefore be coupled.

In order to make the situation clearer to myself, I took two pieces of one fourth inch rubber tubing, eighteen inches long, and marked off, with ink, lengths of one inch. Each tube represented one chromosome of a homologous pair, and the inch lengths represented the factors. I marked the factors on one chromosome with odd numbers, 1, 3, 5, 7, etc., to 35. This chromosome I called maternal. The factors of the other I marked with 2, 4, 6, 8, etc., to 36, and called this chromosome

## TABLE IX.

The two vertical columns named *r* (right) and *l* (left) contain all the factors of both parents. Each column represents one gamete and contains that half of the factors not found in its fellow. Odd numbers represent maternal, even numbers paternal characters.

| r | l | r | l | r | l | r | l | r | l | r | l | r | l |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| No turn | | $\frac{3}{8}$ turn | | $\frac{1}{2}$ turn | | turn $\frac{5}{8}$ | | $\frac{3}{4}$ turn | | $\frac{7}{8}$ turn | | One turn | |
| 1 | 2 | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 3 | 1 | 2 |
| 3 | 4 | 3 | 4 | 3 | 4 | 3 | 4 | 3 | 4 | 3 | 4 | 3 | 4 |
| 5 | 6 | 5 | 6 | 5 | 6 | 5 | 6 | 5 | 6 | 5 | 6 | 5 | 6 |
| 7 | 8 | 7 | 8 | 7 | 8 | 7 | 8 | 7 | 8 | 7 | 8 | 7 | 8 |
| 9 | 10 | 9 | 10 | 9 | 10 | 9 | 10 | 9 | 10 | 9 | 10 | 9 | 10 |
| 11 | 12 | 11 | 12 | 11 | 12 | 11 | 12 | 11 | 12 | 11 | 12 | 12 | 11 |
| 13 | 14 | 13 | 14 | 13 | 14 | 13 | 14 | 14 | 13 | 14 | 13 | 14 | 13 |
| 15 | 16 | 15 | 16 | 15 | 16 | 16 | 15 | 16 | 15 | 16 | 15 | 16 | 15 |
| 17 | 18 | 17 | 18 | 17 | 18 | 18 | 17 | 18 | 17 | 18 | 17 | 18 | 17 |
| 19 | 20 | 19 | 20 | 20 | 19 | 20 | 19 | 20 | 19 | 20 | 19 | 20 | 19 |
| 21 | 22 | 21 | 22 | 22 | 21 | 22 | 21 | 22 | 21 | 22 | 21 | 22 | 21 |
| 23 | 24 | 24 | 23 | 24 | 23 | 24 | 23 | 24 | 23 | 24 | 23 | 24 | 23 |
| 25 | 26 | 26 | 25 | 26 | 25 | 26 | 25 | 26 | 25 | 26 | 25 | 25 | 26 |
| 27 | 28 | 28 | 27 | 28 | 27 | 28 | 27 | 28 | 27 | 28 | 27 | 27 | 28 |
| 29 | 30 | 30 | 29 | 30 | 29 | 30 | 29 | 30 | 29 | 29 | 30 | 29 | 30 |
| 31 | 32 | 32 | 31 | 32 | 31 | 32 | 31 | 32 | 31 | 31 | 32 | 31 | 32 |
| 33 | 34 | 34 | 33 | 34 | 33 | 34 | 33 | 34 | 33 | 33 | 34 | 33 | 34 |
| 35 | 36 | 36 | 35 | 36 | 35 | 36 | 35 | 36 | 35 | 35 | 36 | 35 | 36 |

paternal. Thus 1 and 2 represented the two members of a pair of homologous factors, as did also 3 and 4, 5 and 6, etc., to 35 and 36, in every case the odd number representing the maternal, and the following even number the corresponding paternal factor.

I now secured the ends of the chromosomes so that the proper factors stood opposed to each other and began to twist the chromosomes.

It was at once apparent that if the twisting should not vary in the members of one species, coupling would be invariable, nor would the coupling be that representing either parent alone, but both, and the combination of factors would be always the same. This is shown in Table IX. In this table the vertical columns represent the gametes formed when a splitting follows the number of twists named at the top of the column. In each case there are two different combinations of gametes; one formed on the left and one on the right side of the split.

A study of the above table will show that if there be, for instance, no turn and the split falls between the two chromosomes all the factors in the gamete on the right will be maternal. If there be three eighths of a turn, the odd-numbered factors from 1 to 21 (maternal) and the even-numbered factors from 24 to 36 (paternal) will always be in the gamete on the right. And so in every case, if the amount of twist be constant, the factors present in any gamete will be constant. This will be true even if the factors are of different lengths, and the twisting not uniform for all parts of the same chromosome, if only the lack of uniformity be constant in all the members of the species.

Now, the nature of the twisting and the amount of variation that occurs can only be solved, if at all, by the cytologist. On the face of the question as so far presented it must be that variation in the twist occurs, or there would, on the basis of the theory here discussed, be no such thing as " independent mendelizing," but a constant coupling. My question is therefore, " What are the facts concerning this twisting? How uniform is it? " For I conceive it to be possible that if the twisting be nearly definite, coupling of certain factors would generally occur, and would depend not entirely on the nearness together of the factors, but on the amount of the twist, and on the side of the splitting

double chromosome on which any factor should be thrown by the twist. As Morgan points out, the chances of separation are not so great for factors which lie near each other as for those far from each other, though coupling would not necessarily imply that the factors should lie in one segment of the twisted chromosome. According to this idea the factors for wing length, as explained by Morgan in the paper in the *Journal of Experimental Zoölogy* for November, 1911, may not be closely approximated to those for eye color and body color.

### SUMMARY.

1. The factors for red and for white eye color and for normal and yellow body color in *Drosophila* have been the subjects of investigation in these experiments.

2. In the $F_2$ generation the factors for eye color and body color appear to a great extent associated in the same combinations that were present in the grandparents, the interchanging taking place only once to nearly eighty cases where there is no inter-changing.

3. The absence in a fly of certain characters found in the normal wild fly, seem to render it less fertile, or at least such flies hatch in smaller numbers than do those in which such characters are present.

4. These facts are in accord with the principles and theories advanced by Morgan, and can be explained on a theory based on (1) the relative positions of factors in the chromosomes, (2) the twisting of homologous chromosomes about each other in gameto-genesis, and (3) their subsequent splitting in one plane.

5. Further cytological evidence bearing on the above theory is much to be desired.